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MAMMALIAN SPECIES 43(886):177–189

Steno bredanensis (Cetacea: Delphinidae)

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Abstract: *Steno bredanensis* (Cuvier in Lesson, 1828) is a small odontocete commonly called the rough-toothed dolphin. A slender, gray dolphin with a slightly darker cape, this species is most easily distinguished from other small delphinids by a gradually sloping forehead and a long rostrum. It is the only species in the genus *Steno*. Despite reports of sightings or stranded specimens from all tropical and subtropical oceans, the species is thought to typically occur in low abundance. The conservation status of *S. bredanensis* is poorly known.

Key words: cetacean, dolphin, marine mammal, odontocete, rough-toothed dolphin

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Steno Gray, 1846

Steno Gray, 1846:43. Type species *Delphinus rostratus* Cuvier, 1833 (= *Delphinus bredanensis* Cuvier in Lesson, 1828), by monotypy.
Glyphidelphis Gervais, 1859:301. Type species *Delphinus rostratus* Cuvier, 1833 by monotypy.

CONTEXT AND CONTENT. Order Cetacea, suborder Odontoceti, family Delphinidae, subfamily Steninae. The genus *Steno* is monotypic.

Steno bredanensis (Cuvier in Lesson, 1828)
Rough-toothed Dolphin

Delphinus rostratus (Desmarest, 1817:160). Type locality "Paimpol, Brittany, France." Preoccupied by *Delphinus rostratus* Shaw, 1801.
Delphinus frontatus (Cuvier, 1823:278). Type locality unknown.
Delphinus bredanensis Lesson, 1828:206. Replacement name for *Delphinus rostratus* Desmarest, 1817; preoccupied by *Delphinus rostratus* Shaw, 1801.
Delphinus planiceps Schlegel, 1841:27, tab IV. A replacement name for *Delphinus bredanensis* van Breda, 1829.
Delphinorhynchus santonicus Lesson, 1836:330. Type locality "Ile d'Aix, mouth of the Charente River." Type based on a stranded individual that was not preserved.
Delphinus compressus (Gray, 1843:105). Nomen nudum.
Steno rostratus Gray, 1846:30, 46. Renaming of *Delphinus rostratus* Desmarest, 1817.
Steno compressus Gray, 1846:43, pl. 27. Type locality unknown.
Delphinus (*Steno*) *perspicillatus* Peters, 1877:360, Taf. 3. Type locality "im atlantischen Ocean, in 32° 29' 7 S. B. und 2° 1' W. L. Gr. harpunirt wurde."
Steno bredanensis: Miller and Kellogg, 1955:657–658. First use of current name combination.
Delphinus chamissonis: Herskovitz, 1966:17. Not *Delphinus chamissonis* Wagner, 1846.

CONTEXT AND CONTENT. Context as for genus. Species is monotypic.



Fig. 1.—Pubertal male *Steno bredanensis* from Dolphin Quest French Polynesia, photographed in 2000. Dolphin Quest French Polynesia (The Moorea Dolphin Center) is a captive-care facility that houses dolphins in French Polynesia, located in the South Pacific. Used with permission of the photographer Cecile Gaspar.

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Fig. 2.—Dorsal, ventral, and lateral views of the skull and lateral view of mandible of an adult female *Steno bredanensis* (National Museum of Natural History 572792). Note that view of the right mandible has been reversed to align it with the cranium. Specimen is from Wreck Island, Virginia. Condylobasal length of skull is 503 mm. Used with permission of the photographer Michael Potter.

NOMENCLATURAL NOTES. The historical nomenclature of *S. bredanensis* is particularly confusing. Schevill (1987) and Flower (1884) have both provided accounts of this history. The fate of the type specimen is unclear and it may have been lost. The relationship between *S. perspicillatus* and *S. bredanensis* is addressed by Fraser (1966).

A series of illustrations of the external appearance and skull of the specimen of *Delphinus bredanensis* from Brest that Lesson (1828:figure 1) described and an account of Cuvier's role in the historical nomenclature of *S. bredanensis* is provided by van Breda (1829:235, 236, 238, plate I—figures 1–6, plate II—figures 1 and 2). This is the paper that is miscited by Hershkovitz (1966:16), following Flower (1884:484) as the authority for *D. planiceps* van Breda. The trivial name *planiceps* does not occur in van Breda (1829).

Hershkovitz (1966:17) follows Wagner's (1846) attribution to "Wiegmann, 1841 (or earlier)" based on Wagner's labeling of his plate CCCLIX (359) as "Delphinus Chamissonis Wiegm." We surmise that Wagner had seen a manuscript by Wiegmann because we were not able to locate the record in the published literature.

DIAGNOSIS

In the wild, *Steno bredanensis* can most easily be distinguished from other small delphinids by a forehead that gradually slopes into a long and slender rostrum, lacking the demarcation that separates the melon and beak (Fig. 1). Although *Stenella* and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) have a similarly long rostrum, they have the clear demarcation that is absent in *S. bredanensis*. The bottlenose dolphin (*T. truncatus*) has a much shorter rostrum and a dorsal fin that is less erect but may still be confused with *S. bredanensis* (Jefferson and Leatherwood 1993; Perrin et al. 2007).

The color pattern appears to vary according to geographic location and age of the individual (Miyazaki and Perrin 1994). *S. bredanensis* is gray in color with a slightly darker gray cape and often has distinctive white lips (Baker 1987; Jefferson and Leatherwood 1993). The darker cape is apparent from above the eye to the dorsal fin, gradually widening, and extending down the sides of the animal (Miyazaki and Perrin 1994; Fig. 1). The sides of the animal are typically a lighter gray color, and there may be white, pink, or yellow splotches or scarring on the tip of the rostrum, along the lower jaw, and in the ventral region. The mottled appearance is more frequently seen in older individuals, whereas uniform shades of gray are common in younger animals (Miyazaki and Perrin 1994).

The skull (Fig. 2) may be confused with that of the Indo-Pacific humpback dolphin (*Sousa chinensis*) or *Stenella* but the skull of *S. bredanensis* is generally longer than those of *Stenella* (condylobasal length $>$ 472 mm—Miyazaki and Perrin 1994). The rostrum of *S. bredanensis* is also long, approximately 60% of the condylobasal length, similar to the ratio between condylobasal length and rostrum in the spinner dolphin (*Stenella longirostris*), Pantropical spotted dolphin (*Stenella attenuata*), and striped dolphin (*Stenella coeruleoalba*—Perrin and Gilpatrick 1994; Perrin and Hohn 1994; Perrin et al. 1994). The mandibular symphysis of *S. bredanensis* is about one-third the length of the mandible, whereas the mandibular symphysis does not generally exceed 30% of the mandibular length in *Sousa* (Ross et al. 1994). The orbits of *S. bredanensis* also are relatively large ($>$ 13% of condylobasal length) compared to *Sousa*. There are 19–26 teeth on each side in the upper jaw and 19–28 teeth in the lower jaw (Miyazaki and Perrin 1994). Tooth counts also can be used to distinguish between *S. bredanensis* and *Sousa* because *S. chinensis* has 30–38 teeth in each jaw and alveoli

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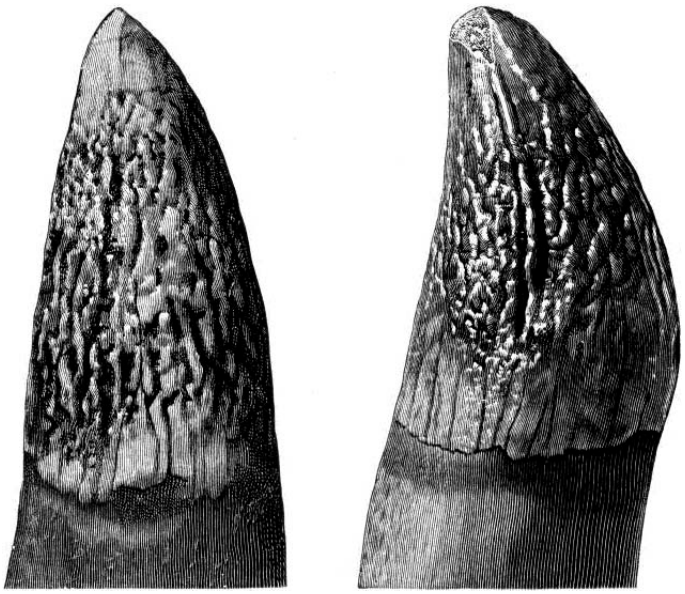


Fig. 3.—Magnified diagram of teeth ridges of *Steno bredanensis* reprinted from Neuville (1928), illustrating the fine tooth ridges that are characteristic of *S. bredanensis.* The tooth is from the middle of the upper jaw; lingual aspect on the left, medial aspect on the right.

that are larger and more widely spaced (Van Waerebeek et al. 1999). The common name comes from fine, longitudinal ridges apparent on the surface of the teeth (Fig. 3). This character can be diagnostic when comparing teeth from *S. bredanensis* side by side with teeth from other delphinids.

GENERAL CHARACTERS

Steno bredanensis is sexually dimorphic, with males larger than females (Miyazaki and Perrin 1994; West 2002). The total length of 64 male and female adult specimens compiled from the Pacific and Atlantic oceans and the Mediterranean Sea ranged from 209 to 265 cm (Miyazaki and Perrin 1994). Larger specimens are reported from Brazil, where maximum length for a male is 283 cm and for a female 270 cm (Siciliano et al. 2007).

Average body mass for *S. bredanensis* is reported as 130 kg (Watson 1981). Fourteen specimens ranged from 90 to 155 kg (Miyazaki and Perrin 1994). The total body length (L)–total body weight (W) relationship for a combination of 15 males and females is estimated as $L = 3.123 + 2.805 \log W$ ($r = 0.999$—Miyazaki and Perrin 1994).

Selected external measurements of adult specimens compiled from the Pacific and Atlantic oceans and the Mediterranean Sea were as follows (cm): tip of upper jaw to apex of melon, 10–14 ($n = 15$); tip of upper jaw to end of gape, 22–37 ($n = 35$); tip of upper jaw to umbilical scar, 79–121 ($n = 25$); tip of upper jaw to tip of dorsal fin, 129–131 ($n = 2$); girth at axilla, 100–110 ($n = 17$); anterior length of flipper, 36–49 ($n = 36$); width of flipper, 13–17 ($n = 33$); span of flukes, 46–65 ($n = 35$); width of fluke, 14–23 ($n = 27$); and height of dorsal fin, 18–28 ($n = 23$—Miyazaki and Perrin 1994).

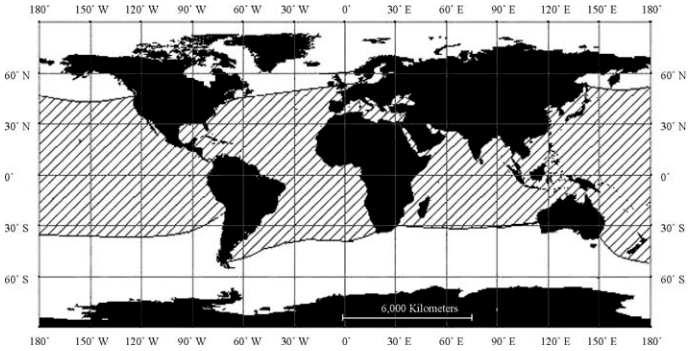


Fig. 4.—Geographic distribution of *Steno bredanensis*.

The characteristically long rostrum of *S. bredanensis* is apparent in the skull and mandible (Fig. 2). Cranial measurements compiled from a number of sources for adult specimens from the Atlantic and Pacific oceans and the Mediterranean Sea were as follows (mm): condylobasal length, 472–555 ($n = 66$); length of rostrum, 274–343 ($n = 59$); width of rostrum at base, 87–119 ($n = 58$); width of rostrum at one-half its length, 38–64 ($n = 58$); preorbital width, 169–196 ($n = 6$); postorbital width, 202–239 ($n = 6$); greatest width of premaxillaries, 75–89 ($n = 10$); parietal width, 162–184 ($n = 7$); length of temporal fossa, 86–119 ($n = 40$); height of temporal fossa, 80–105 ($n = 40$); number of teeth in each side of upper jaw, 19–26 ($n = 81$); and number of teeth in each side of lower jaw, 19–28 ($n = 82$—Miyazaki and Perrin 1994). Cranial measurements obtained by 2 of the authors (KLW and JGM) from another 23 adults from the Atlantic and the Pacific oceans are almost entirely within these ranges except for the following (mm): preorbital width, 163–185; postorbital width, 192–215; greatest width of premaxillaries, 72–85; and parietal width, 133–160.

DISTRIBUTION

Steno bredanensis is found worldwide with reports from the Atlantic, Pacific, and Indian oceans, typically in warm temperate, subtropical, or tropical waters (Fig. 4). In the southwestern Atlantic the most southerly report of the species is from Patagonia in Argentina but is based on a solitary skull at the Academy of Natural Sciences (Philadelphia, Pennsylvania) collected in the late 1800s (catalog number ANSP 23360). The species is reported on many occasions from Brazil (Pinedo and Castello 1980; Rice 1998; Siciliano et al. 2007). In the Caribbean Sea, *S. bredanensis* is reported throughout the Gulf of Mexico and along the coastal United States north to Virginia (Miyazaki and Perrin 1994).

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The most northerly records from the northeastern Atlantic are from the Scheldt estuary, Belgium, in the North Sea (Booij 2004), and from a stranded specimen in Paimpol, France (Cuvier 1812; Van Beneden 1889). *S. bredanensis* also is reported from Portugal (Busnel and Dziedzic 1966), Spain (Hashmi and Adloff 1991), the Mediterranean Sea (Watkins et al. 1987), Macronesia (Bronner et al. 2003; Steiner 1995), and the western coast of Africa from Mauritania to Namibia (Addink and Smeek 2001; Bronner et al. 2003; Perrin and Van Waerebeek 2007; Ross et al. 1985; Steiner 1995).

A stranding of *S. bredanensis* is reported off the coast of southeastern Africa near the Zambesi River (Best 1971; Brownell 1975). However, this may have been a mistake, because it appears that this same specimen was later described as a junior synonym for *Sousa plumbea* (Brownell 1975; *plumbea* is currently considered a synonym of *Sousa chinensis*). *S. bredanensis* is reported from Tanzania and Kenya, but not enough detail is provided to evaluate the validity of this report (Davies and Vanden Berghe 1994). It is also found offshore of Somalia, the Aden District, and the Red Sea (Anderson 1891; Ballance et al. 1996; Best 1971; Frazier et al. 1987). The species is found in the Arabian Sea from the Gulf of Oman throughout the Indian Ocean to the Nicobar Islands (Alling 1986; Anderson 1891; Anderson et al. 1999; R. M. Baldwin et al., in litt.; Ballance et al. 1996, 2001; Ballance and Pitman 1998; International Whaling Commission 1994; Leatherwood and Reeves 1989; Van Waerebeek et al. 1999). Strandings are reported from Java, Indonesia (Chasen 1940; Kahn 2001), throughout the South China Sea (Beasley and Jefferson 1997; Chantrapornsyl et al. 1996; Corkeron et al. 2003; Heaney et al. 1998; Parsons 1998; Smith et al. 1997; Yang 1976), to the East China Sea (Wenji 1980).

In the western Pacific there are reports from Japan, the Northern Mariana Islands, and Kiribati (Hobbs and Jones 1993; International Whaling Commission 1994; Jefferson et al. 2006; Miller 2006; Miyazaki 1980). A specimen also was obtained from the Marshall Islands (*Smithsonian Cetacean Distributional Database*, available at http://www.cms.int/reports/WAFCET/WAFCET2/WAFCET2_Report.htm, accessed 25 May 2011).

In the central North Pacific, *S. bredanensis* is commonly sighted throughout the Hawaiian Archipelago (Baird et al. 2008). In the eastern Pacific this species is described as part of the fauna in the Bering Sea; however, this report is not substantiated by a positively identified specimen (Collins et al. 1945). The most northerly reports on the west coast of the United States are from Washington and Oregon, but these strandings are thought to represent vagrants outside of normal species range (Ferrero 1994; Norman et al. 2004). *S. bredanensis* is reported from California (Daugherty and Schuyler 1979; Woodhouse 1991), down the coast of Mexico (Estrella 1994; Heyning 1986; Perrin and Oliver 1982; *Smithsonian Cetacean Distributional Database* [http://www.cms.int/reports/WAFCET/WAFCET2/WAFCET2_Report.htm, accessed 25 May 2011]) through Central America (Perrin and Kashiwada 1989), from the Pacific coast of Colombia (Holt and Jackson 1987; Mora-Pinto et al. 1995; Rodriguez 1989), and from the Galapagos Islands (Orr 1965). The most southerly report along the South American coast is from Chile at 24°S (Van Waerebeek and Guerra 1988). *S. bredanensis* is commonly sighted in the eastern tropical Pacific but not in high abundance (Au and Perryman 1985; Hewitt 1985; Wade and Gerrodette 1993; Wahlen et al. 1986). *S. bredanensis* is relatively abundant in the Society Islands, French Polynesia, and is occasionally sighted about 1,440 km to the north in the Marquesas, French Polynesia (Gannier 2000, 2002; Gannier and West 2005; Laran and Gannier 2001). There are also reports from New Zealand waters (Baker 1983), the Solomon Islands, Papua New Guinea (Brownell et al. 1978), and Australia (Baker 1983; Bannister et al. 1996; Ogawa 1938).

FOSSIL RECORD

Steno fossils are uncommon but they are reported from the lower and middle Pliocene in Europe (Marcuzzi and Pilleri 1971). Fossil records for cetacean history extend back 50 million years and odontocetes most likely originated approximately 34–35 million years ago (Fordyce 2002). Fossil records for the Delphinidae date back to the late Miocene, possibly 11 million years ago, in both Europe and North America (Barnes et al. 1985; Fordyce 2002).

FORM AND FUNCTION

Form.—The vertebral formula of *Steno bredanensis* is 7 C, 13 T, 15–16 L, 30–31 Ca, total 65–67, with atlas and axis fused (Miyazaki and Perrin 1994; Tinker 1988). A reduced number of vertebrae is reported for 1 adult specimen with a vertebral formula of 7 C, 12 T, 15 L, 28 Ca, total 62 (Buchholtz and Shur 2004; Buchholtz et al. 2005). There are 21 or 22 chevron bones, and phalangeal count is I (3), II (8–9), III (6–7), IV (3), and V (2—Tinker 1988). We have observed 0–1 floating ribs, 6–7 single-headed ribs, and 5–7 double-headed ribs.

Much of what is known of the anatomy comes from a monograph by Neuville (1928). He described the soft anatomy of the thyroid, thymus, lymphatic system, lungs, stomach, spleen, and pancreas. The liver of *S. bredanensis* is bell shaped with 2 surfaces, a convex facies diaphragmatica and a facies visceralis that is divided into 2 lobes (Hojo and Mitsuhashi 1975). There is coronal duplication in teeth (Neuville 1928). Emmetropia, a state of perfect vision where the eye is relaxed while focused on distant objects, and movability of the operculum were observed in air for captive *S. bredanensis* (Dral and Duok van Heel 1974). A diagram of the tympanic bones is provided in Pilleri et al. (1989). The

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nasal sac system is described as similar to that of other delphinids (Mead 1975; Purves 1966).

Masses of selected organs are available from Japanese specimens that ranged between 112.4 and 154.7 kg in total body weight: brain, 1,170–1,602 g (n = 14); heart, 605–1,080 g (n = 15); lungs, 1,640–3,934 g (n = 15); liver, 1,720–3,432 g (n = 15); left kidney, 489–826 g (n = 14); right kidney, 500–830 g (n = 15); spleen, 34–178 g (n = 15); pancreas, 110–191 g (n = 14); and intestines, 1,922–3,480 g (n = 15—Miyazaki and Perrin 1994).

Function.—A physiological study of a captive *Steno bredanensis* compared renal function at 4 and 18 h after a meal. At 4 h after a meal, a higher urine flow rate (2.8 ml/min at 4 h compared to 1.3 ml/min at 18 h), glomerular filtration rate (169 ml/min at 4 h compared to 131 ml/min at 18 h), and urea concentration (82.4 ml/min at 4 h compared to 53.1 total body weight at 18 h) were observed (Malvin and Rayner 1968). Body temperature of an individual in Hawaii monitored with telemetry over 29 hours was 36.5–37.6°C and mean respiration rate was 2.8 breaths per minute (Whittow et al. 1978).

Hemoglobin of *S. bredanensis* is categorized as type V, having 2 distinct hemoglobin bands (Baluda et al. 1972). Blood chemistry and hematology parameters from 17 *S. bredanensis* were compared according to health status (sick versus healthy). Sick dolphins have higher levels of aspartate aminotransferase, alanine aminotransferase, lactate dehydrogenase, bicarbonate, and globulins than healthy ones, whereas healthy individuals have higher levels of alkaline phosphatase and protein than sick *S. bredanensis* (Baluda et al. 1972). Total white blood cell counts are lower in healthy than in sick *S. bredanensis*, and averaged $7.57 \times 10^3/mm^3$ in 157 samples collected from 8 healthy individuals (C. A. Manire et al., in litt.). A stranded calf in Brazil that died had a white blood cell count of $4.4 \times 10^3/mm^3$ and low values of aspartate aminotransferase, alanine aminotransferase, creatinine, and glucose (Bastos et al. 2003). Hematocrit from a single individual is reported at 50% (Malvin and Rayner 1968) and averaged 47.8% in 170 samples collected from 8 healthy individuals (C. A. Manire et al., in litt.). Immunoglobulin classes also have been identified from sera (Nash and Mach 1971).

ONTOGENY AND REPRODUCTION

Length at birth is probably about 100 cm; the largest reported fetus measured 93 cm and a stranded calf measured 106 cm (Bastos et al. 2003; Miyazaki and Perrin 1994; West 2002). Growth is rapid during the first 5 years of life, with individuals reaching at least 200 cm by 5 years of age (Miyazaki and Perrin 1994; West 2002). Asymptotic body lengths are reached at about 231–258 cm, depending on geographic region. In Japan, *Steno bredanensis* reaches asymptotic lengths at 231 cm and in Florida at 239 cm (Miyazaki 1980; M. K. Stolen, in litt.). We observed asymptotic lengths of 210–231 cm (n = 62) in a group of specimens from the Atlantic and Pacific oceans. In Brazil, asymptotic length is greater, estimated at 258 cm (n = 14—Siciliano et al. 2007).

In Brazil, a large *S. bredanensis* aged at 6 years old was pregnant (Siciliano et al. 2007). Females sampled from the Atlantic and Pacific oceans begin a gradual process of sexual maturation between 3 and 6 years of age (with age determined from undecalcified dentinal layers) and reach sexual maturity by 8–9 years (West 2002). Females attain sexual maturity at a body length of 212–219 cm and a body mass of 101–108 kg (West 2002). Our observations confirm data suggesting that females reach sexual maturity at about 10 years of age and at 210 cm in length in Japan (unpublished data cited in Miyazaki and Perrin 1994).

Males sampled from the Atlantic and Pacific reach sexual maturity between 5 and 10 years of age, at a body length of 211–216 cm and a body mass of 83–102 kg (West 2002). A stranded male estimated at 7 years of age was considered immature because of small testes mass of 23.3 g (Ferrero 1994), and 2 males 14 and 21 years of age (determined from both decalcified and undecalcified dentinal layers) were sexually mature with testes that contained sperm (Miyazaki 1980). Immature males have testes masses $\leq$ 54.3 g, whereas sperm-producing testes of mature males have masses of 66–1,500 g (Miyazaki 1980; West 2002).

Females generally attain physical maturity at a younger age and smaller size than males. In females sampled from the Atlantic and Pacific, physical maturity, as defined by fusion of the vertebral epiphyses, is attained at about 9–12 years of age, at a body length of 210–217 cm, and a body mass of 85–101 kg (n = 13—West 2002). Males attain physical maturity (vertebral epiphyseal fusion) at a wide range of ages. One male was physically mature at only 5 years of age, whereas a 14-year-old individual was still immature (in a sample of 15 males—West 2002). A previous report suggested epiphyseal fusion in males at 16 years of age (Miyazaki and Perrin 1994). Males sampled from the Atlantic and Pacific reach physical maturity at 227–231 cm and 119–130 kg (West 2002). No information is available regarding reproductive seasonality or the duration of gestation or lactation.

ECOLOGY

Steno bredanensis may be solitary but is often found in groups of various sizes. The largest report of group size was estimated at 160 individuals in the Mediterranean (Watkins et al. 1987). Group size averaged 10.8 individuals in French Polynesia where solitary sightings and group sizes between 2 and 35 individuals were observed (Gannier and West 2005). Group size averaged 10 individuals from 44 sightings in Hawaii with a range of 2–90 dolphins (Baird et al. 2008). In the Canary Islands, groups are most commonly composed of

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10–20 animals ($\bar{X}$ = 16.8), although groups of up to 50 individuals are sighted (Ritter 2002).

Large-scale vessel surveys in the eastern tropical Pacific estimate the abundance of *S. bredanensis* at 145,900 (coefficient of variation [*CV*] = 0.32—Wade and Gerrodette 1993). Vessel surveys conducted in both oceanic waters and off the outer continental shelf in the northern Gulf of Mexico estimate 2,223 individuals (*CV* = 0.41—Fulling et al. 2003; Mullin and Fulling 2004; Waring et al. 2005). J. R. Mobley (in litt.) conducted aerial surveys within 25 nautical miles of the main Hawaiian Islands and estimated a population size of 123 individuals (*CV* = 0.63). This is an underestimate of population size because at least 337 distinct individuals were photographically identified over a 6-year period throughout the Hawaiian Islands. However, this study still suggests a relatively small population size as well as site fidelity because of frequent within and between year resightings (Baird et al. 2008). The estimated abundance of *S. bredanensis* throughout the entire Exclusive Economic Zone of Hawaii, including waters > 25 nautical miles from the main Hawaiian Islands, and those in the northwestern Hawaiian Islands is 8,709 individuals (*CV* = 0.45—Barlow 2006). It is not known whether the animals occurring around Hawaii are part of the same stock as those in the eastern tropical Pacific.

Steno bredanensis is commonly found in shallow nearshore, deep offshore, and oceanic waters. There are many reports from shallow waters of coastal Brazil and Honduras (Carvalho Flores and Ximenez 1997; Kuczaj and Yeater 2007; Lodi 1992). In French Polynesia, this species is most frequently sighted in 1,000- to 2,000-m depths, 1.8–5.5 km from shore (Gannier and West 2005). Similarly in Hawaii, sightings are most common in depths > 1,500 m and > 3 km from shore (Baird et al. 2008). In the Canary Islands, mean sighting depth is slightly > 500 m and mean distance is 4.4 km from shore (Ritter 2002). In French Polynesia, Hawaii, and the Canary Islands *S. bredanensis* has been identified as relatively abundant. All of these locations are characterized by steep volcanic islands that are surrounded by deep oceanic waters close to the coast.

Steno bredanensis is reported to form mixed schools with bottlenose dolphins, melon-headed whales (*Peponocephala electra*), false killer whales (*Pseudorca crassidens*), Fraser's dolphins (*Lagenodelphis hosei*), humpback whales (*Megaptera novaeangliae*), short-finned pilot whales (*Globicephala macrorhynchus*), spinner dolphins, and Atlantic spotted dolphins (*Stenella frontalis*—Baird et al. 2008; Gannier and West 2005; Leatherwood and Reeves 1983; Perrin and Walker 1975; Ritter 2002; Scott and Chivers 1990; Watson 1981).

There are no confirmed reports of predation but it is likely, based on anecdotal evidence, that sharks and killer whales (*Orcinus orca*) prey on *S. bredanensis*. An attack by a group of sharks is theorized as the reason why an individual beached itself in Texas (Schmidly and Melcher 1974). In Hawaii, a captive *S. bredanensis* left trainers in the midst of open ocean experiments when several small sharks, including a 4-m shark, were observed in the area (Norris et al. 1965). Scarring from bites of the cookie-cutter shark (*Isistius brasiliensis*) is common (Addink and Smeenk 2001; Baker 1987).

Diet has been inferred from stomach contents or from field observations of suspected foraging. In most cases, stomach contents are from stranded individuals and may not be representative of the diet of healthy *S. bredanensis*. Stomach contents from strandings in Hawaii consisted primarily of nearshore species, including silverside fish (*Pranesus insularum*), saury (*Cololabis adocetus*), houndfish (*Tylosurus crocodilus*), and an unidentified squid (Shallenberger 1981). We observed head and tail of a houndfish in separate stomach samples from this same stranding. Stomach contents from 3 individuals stranded off Oregon and Washington included top smelt (*Atherinops affinis*), jack smelt (*Atherinops californiensis*), and 2 species of squid (*Ommastrephes bartrami* and *Onychoteuthis borealijaponia*—Ferrero 1994). Stomach contents of stranded specimens in Florida include the blanket octopus (*Tremoctopus violaceus*) and, in a few cases, a significant amount of algae (*Sargassum filipendula*—Layne 1965). The slender inshore squid (*Loligo plei*) was reported as the primary cephalopod prey from Brazilian specimens (dos Santos 2001). A cutlass fish (*Trichiurus lepturus*) and an unidentified bone fish also were reported among solid food remains from Brazil (Di Beneditto et al. 2001; Ott and Danilewicz 1996). Remains include mollusks and fish from the eastern tropical Pacific (Perrin and Walker 1975).

Foraging by *S. bredanensis* has been observed in the field on a number of occasions. In the Azores underwater snipefish (*Macrorhamphosus scolopax*) were fed upon simultaneously by both *S. bredanensis* and Cory's shearwaters (*Calonectris diomedea borealis*—Steiner 1995). The dolphins were observed taking turns feeding from an aggregation of the snipefish that formed a ball about 0.5 m in diameter. However, no dolphins were observed keeping the fish ball together (Steiner 1995). In the southwestern Atlantic off the Brazilian coast, in the Abrolhos Bank breeding ground, *S. bredanensis* was observed catching a diskfish (Echeneidae—Wedekin et al. 2004). In both Hawaii and in the eastern tropical Pacific adult-sized mahi-mahi (*Coryphaena hippurus*) were reported in the mouth of *S. bredanensis* (Brower 1979; Pitman and Stinchcomb 2002). We observed mahi-mahi among the stomach contents of a specimen incidentally caught in the eastern tropical Pacific.

Helminths described in *S. bredanensis* include cestodes, nematodes, trematodes, and acanthocephalans. Cestodes include *Tetrabothrius forsteri*, *Strobilocephalus triangularis*, and *Trigonocotyle prudhoei* (Arvy 1982; Delyamure 1955; Forrester and Robertson 1975; Gibson and Harris 1979;

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Layne 1965). We observed the cestodes *Phyllobothrium* and *Monorhygma* in stranded specimens from both Hawaii and Virginia. Trematodes found in *S. bredanensis* include *Campula palliata*, *Pholeter gastrophilus*, *Synthesium tursionis*, and *Braunina cordiformis* (Forrester and Robertson 1975; Ott and Danilewicz 1996), and we observed trematodes of the genus *Nasitrema.* Nematodes reported from *S. bredanensis* include *Anisakis* and *Crassicauda* (Forrester and Robertson 1975). The only acanthocephalan reported in *S. bredanensis* is *Bolbosoma capitatum* (Gibson and Harris 1979). An isopod ectoparasite of a fish, *Nerocila*, was found in the stomach of a stranded *S. bredanensis* in southern Brazil (Ott and Danilewicz 1996).

Solitary and mass strandings have occurred in most regions of the world where this species is found. In a mass stranding in Cap Vert, Senegal, 25 of 28 animals were males, indicating an extremely unbalanced sex ratio (Cadenat 1949). We examined specimens at the National Museum of Natural History, Washington, D.C., from a mass stranding in 1976 of 17 individuals from Hawaii and 16 from Virginia Beach, Virginia, that had beached later that same year. In 2002, 14 animals were found dead at Wreck Island, Virginia (West 2002). Historical and recent mass strandings have been reported for Florida, including 16 near Rock Island in 1961 (Layne 1965). Recent strandings have occurred along both the Gulf of Mexico and the Atlantic coasts, as well as in the Florida Keys (C. A. Manire, in litt.; H. L. Rhinehart et al., in litt.). Chronic progressive viral arteritis is a suspected cause behind some of the Florida strandings (H. L. Rhinehart et al., in litt.).

HUSBANDRY

Steno bredanensis has been held in captive facilities around the world, including in the United States, Hong Kong, Japan, Europe, and French Polynesia (Collet 1984; Miyazaki 1980; Parsons 1998; Reeves and Leatherwood 1984; West 2002). In the 1950s, *S. bredanensis* was captured in the Mediterranean Sea and near the Madeira Archipelago, Portugal, for a physiological laboratory (Collet 1984). In the 1960s and 1970s in Japan, individuals of this species were captured and held in a captive facility for at least 4 months (Miyazaki 1980; Nishiwaki 1967). As of 1981, 23 individuals had been collected near Hawaii and held at Sea Life Park (Waimanalo, Hawaii). Five of these either escaped or were released. One of the individuals had initially stranded and then survived in captivity for at least 6 years (Reeves and Leatherwood 1984; Tomich 1986). In 1971, a viable hybrid of a bottlenose dolphin and *S. bredanensis* was born at Sea Life Park, Hawaii (Dohl et al. 1974). At least 5 *S. bredanensis* were held in captivity on the island of Moorea in French Polynesia for up to 6 years during the 1990s. One was a stranded calf that lived for at least 3 years in captivity (West 2002). *S. bredanensis* also has been rehabilitated in Florida, where 14 individuals were treated following several separate stranding events (C. A. Manire et al., in litt.). A stranded specimen in China was cared for at Ocean Park Hong Kong (R. E. Kinoshita; in litt.).

BEHAVIOR

Steno bredanensis commonly forms subgroups that may be a part of a larger group (Kuczaj and Yeater 2007; Ritter 2002). These tight but dynamic subgroups are often composed of 2–8 individuals involved in synchronous behavior. The social organization may be of fission–fusion type (Kuczaj and Yeater 2007; Ritter 2002). Association patterns have demonstrated strong social bonds, especially between mothers and calves or juveniles (Kuczaj and Yeater 2007). Skimming along at the surface is a common behavior (Jefferson 2002; Jefferson and Leatherwood 1993; Leatherwood and Reeves 1983). Surface swimming has been categorized in Honduras and the Canary Islands as traveling (21–27%), resting (4–10%), or milling (9–24%—Kuczaj and Yeater 2007; Ritter 2002). Play with objects (7%) and sexual behavior (4%) were less commonly observed (Kuczaj and Yeater 2007). In other locations, *S. bredanensis* is known for a propensity to associate or play with marine life or flotsam such as logs, plywood, and plastic bags (Brower 1979; Jefferson 2002; Leatherwood et al. 1982; Pitman and Stinchcomb 2002; Ritter 2002; Steiner 1995). Reports of cooperative feeding among group members also are common; they have been observed engaging in cooperative fish-herding techniques (Addink and Smeenk 2001) and appeared to take turns approaching a small aggregation of snipefish (Steiner 1995). Group feeding has been frequently observed in the Canary Islands and Honduras (Kuczaj and Yeater 2007; Ritter 2002).

Captive individuals of *S. bredanensis* have earned a reputation as being highly trainable, creative, sociable, and easy for humans to work with (Pryor et al. 1969; Tomich 1969). Many of the behaviors elicited by individuals at Sea Life Park (Waimanalo, Hawaii) were new and unreinforced behaviors that led to complex training sessions (Pryor et al. 1969).

Diving capabilities may be more extreme than observed. *S. bredanensis* is reported to dive as deep as 70 m, where a few individuals rubbed against a hydrophone at this depth (Watkins et al. 1987). The deepest dive of a trained *S. bredanensis* in open water is 30 m. However, this training session ended because the animal became agitated due to the presence of sharks (Norris et al. 1965). This specific individual was able to dive frequently, because it made 51 dives in < 2 h during open-water experiments (Norris et al. 1965). *S. bredanensis* may remain submerged for up to 15 min (Jefferson 2002; Miyazaki and Perrin 1994). While bow-riding (riding the waves produced off the bow or front of a moving vessel) *S. bredanensis* has attained swim speeds of up

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to 16 km/h (Watkins et al. 1987). Although described as only an occasional bow-rider (Leatherwood and Reeves 1983; Leatherwood et al. 1982), there are reports of bow-riding from the Mediterranean Sea, the Azores, the Canary Islands, French Polynesia, Hawaii, and Honduras (Baird et al. 2008; Kuczaj and Yeater 2007; Ritter 2002; Steiner 1995; Watkins et al. 1987; West 2002).

Some observations of mothers, calves, or mother–calf pairs of *S. bredanensis* have been noted from various regions of the world. Twenty-nine percent of the groups sighted in French Polynesia and 16% of those sighted in the Canary Islands include at least 1 calf (Gannier and West 2005; Ritter 2002). Echelon swimming occurs, where calves swim very close to the dorsal fin of the mother and gain a hydrodynamic boost (Addink and Smeenk 2001). Off the coast of Mauritania, in North Africa, a mother provided her calf with assistance during feeding by encouraging the calf to pick up a fish it had dropped (Addink and Smeenk 2001). A stranded calf of *S. bredanensis* in Moorea, French Polynesia, induced lactation in an adult bottlenose dolphin held in the same lagoon (Gaspar et al. 2000). Epimeletic behavior (care-giving behavior by a healthy individual to a compromised or dead individual) has been described in Brazil and the Canary Islands (Lodi 1992; Ritter 2007). In the Canary Islands, a large adult female, which was presumed to be the mother, supported a dead calf at the surface. This mother and dead calf were resighted over several days, and 2 other adults also were observed providing support to the body of the calf (Ritter 2007).

At sea *S. bredanensis* produces extremely brief echolocation clicks in bursts of only 0.1–0.2 s in duration (Watkins et al. 1987). Echolocation clicks have both low- and high-frequency components ranging between 2.7 kHz and 256 kHz. The maximum peak frequency of echolocation clicks is approximately 25 kHz (Norris 1969). This value is low compared to maximum peak frequencies that have been described for other species of delphinids such as the false killer whale (40 kHz), the Risso's dolphin (*Grampus griseus*—50 kHz), the spinner dolphin (60 kHz), and the bottlenose dolphin (110–130 kHz—Au 2000; Ketten 1984; Madsen et al. 2004). Whistles have been recorded with sound frequencies of 3–12 kHz where sequences are approximately 0.5 s in duration (W. E. Evans, in litt.; Watkins et al. 1987). *S. bredanensis* has emitted stereotyped calls during stressful situations (W. E. Evans, in litt.). Based on recordings from 6 sightings, other individuals of *S. bredanensis* remain silent while a member of the group echolocates, suggestive of eavesdropping (Gotz et al. 2005).

GENETICS

Both mitochondrial and nuclear variation indicate that *Steno bredanensis* is a highly distinctive species. Studies using mitochondrial cytochrome-*b* sequences indicate that *S. bredanensis* differs considerably from other closely related species, a finding consistent with placement of this species in a separate genus (Agnarsson and May-Collado 2008; LeDuc et al. 1999; May-Collado and Agnarsson 2006). *Steno* and *Sotalia* are sister taxa, according to Bayesian phylogenetic, maximum-parsimony, maximum-likelihood, and neighbor-joining analyses of cytochrome-*b* sequence variation within family Delphinidae, and they are currently retained in the subfamily Steninae (Agnarsson and May-Collado 2008; LeDuc et al. 1999; May-Collado and Agnarsson 2006). However, recent relationships described from a combination of mitochondrial and nuclear DNA phylogenies suggest that *Steno* and *Sotalia* are not sister taxa and that Steninae may be an artificial grouping. Instead, the combination of mitochondrial and nuclear DNA indicate that *Steno* should be allied with the subfamily Globicephalinae or retained as the sole member of Steninae, and that further study is needed to resolve this issue (Caballero et al. 2008).

Isoenzyme analysis of protein variation indicates a low proportion of polymorphic loci (5.3%) from an analysis of 19 loci from 12 enzymes in a population of *S. bredanensis* in waters off Taiji, Japan (Shimura and Numachi 1987). Average heterozygosity of this same population was 0.007 $\pm$ 0.024 *SE*, which was the lowest of 12 species of odontocetes examined (Shimura and Numachi 1987). Within family Delphinidae, average coefficient of genetic distance for isoenzyme analyses between *S. bredanensis* and 7 other delphinids is 0.379, compared to the distance of 1.004 between *S. bredanensis* and an average of 4 species of phocoenids (Shimura and Numachi 1987). Differentiation among microsatellite results indicates distinct populations of *S. bredanensis* at 2 different island groups in French Polynesia, which supports site fidelity in this region (Oremus 2008).

CONSERVATION

Population size and status of *Steno bredanensis* is poorly known from most regions of the world. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (2011) lists *S. bredanensis* in Appendix II, as a species that is not necessarily now threatened with extinction but that may become so unless trade is closely controlled. The International Union for Conservation of Nature and Natural Resources (2011) considers *S. bredanensis* a species of "Least Concern." Despite this, a number of potential threats have been identified, including fisheries that target *S. bredanensis*, the occurrence of this dolphin as incidental catch, and other types of fishery interactions. Additionally, *S. bredanensis* has been live-captured in small numbers for public display, and it may be vulnerable to the negative effects of contaminant burdens and oceanic debris (Kucklick et al. 2002; Leatherwood and Reeves 1989; Miyazaki 1983; Nishiwaki 1967; Oliveira de Meirelles and Duarte do Rego Barros 2007; Schlais 1984).

Fisheries that target *S. bredanensis* directly are reported from Japan, the Solomon Islands, Papua New Guinea, Sri Lanka, the Caribbean, and West Africa. In Japan, schools of

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S. bredanensis in nearshore waters have been targeted by drive fisheries (those that drive the dolphins into shore and kill them—Nishiwaki 1967). *S. bredanensis* is occasionally present in the fish market in Shiogama, Japan (Whitehead et al. 2000). A group of 23 animals was taken in an Okinawan drive fishery in 1976, but none were taken between the years of 1977 and 1981 (Miyazaki 1983; Nishiwaki and Uchida 1977). In the calendar year 1985, Japanese drive fisheries reported a take of 60 *S. bredanensis* throughout Japan (Anonymous 1987). Although drives of dolphins are reported as rare events, when they do occur, tens of animals may be killed in a single drive (Whitehead et al. 2000). Similarly, native fishermen in the Solomon Islands and Papua New Guinea target entire schools of *S. bredanensis* in drive fisheries (Takekawa 1996; Young and Iudicello 2007). Various dolphin species, including *S. bredanensis*, are caught in Sri Lanka and sold as either dolphin or ''dugong'' meat in local fish markets (Leatherwood and Reeves 1989). At least 7 *S. bredanensis* were confirmed at the main fish market in Trincomalee, Sri Lanka, between 1983 and 1986 (Leatherwood and Reeves 1989). On the Caribbean island of St. Vincent, dolphin fishermen pursue all odontocete species encountered, including *S. bredanensis*, but the total take is unknown (Caldwell and Caldwell 1975; Van Bree 1975). A small fishery that targets *S. bredanensis* was reported from the western coast of Africa (Mitchell 1975). Local fishermen from the Atlantic island of St. Helena have harpooned *S. bredanensis*, but this activity is rare, because the animals are known to be difficult to subdue (Perrin 1985).

Steno bredanensis has been indirectly taken as incidental catch from several locations around the world. These include coastal and offshore Japan (drift-net fishery), Sri Lanka (gill-net fishery), the eastern tropical Pacific (purse-seine fishery), Brazil (gill-net fishery), and the Mediterranean Sea (gill-net fishery—Alling 1986; Anonymous 1987; Hobbs and Jones 1993; International Whaling Commission 1994). The annual number of *S. bredanensis* incidentally caught from any of these locations is generally very low, with the highest report being 18 animals caught in the high seas of Japan in 1990 (Hobbs and Jones 1993; International Whaling Commission 1994). Despite only 6 animals being reported from Brazilian gill-net fisheries in 1990, the magnitude of bycatch for *S. bredanensis* is considered higher than for other small cetaceans in Brazil (International Whaling Commission 1994; Monteiro-Neto et al. 2000; Siciliano 1994).

Steno bredanensis has been captured and subsequently held captive in facilities around the world. However, there are no reports of recent collections of this species for captivity, and it is unknown if past collections had a significant impact on local populations.

Bait stealing by *S. bredanensis* has been reported as a problem for fisheries in Hawaii and may also occur in other regions of the world (Schlais 1984). Fishermen have reported losing 20–50% of bait they set, and this species is blamed for all offshore losses in Kona, Hawaii (B. A. Kuljis, in litt.). There are anecdotal reports of illegal activities (poisoning and shooting) by local fishermen to mitigate their losses. This may have an effect on population numbers of *S. bredanensis* in Hawaiian waters (Schlais 1984).

Chemical contamination of the oceans is a widespread problem and may be particularly threatening to high-level consumers such as dolphins. Low concentrations of dichlorodiphenyltrichloroethane (DDT), dieldrin and trans-nonachlor, and polychlorinated biphenyl levels up to 39 ppm were detected in the blubber, brain, or muscle tissues in 6 of 7 *S. bredanensis* that mass-stranded in Hawaii (O'Shea et al. 1980). In the Gulf of Mexico, levels of persistent organic pollutants in *S. bredanensis* were similar to or lower than those reported from other odontocetes (Kucklick et al. 2002; Struntz et al. 2004). However, *S. bredanensis* has higher percentage ratios of 4,4′-DDT to 4,4′-DDT + 4,4′-dichlorodiphenyldichloroethylene (4,4′-DDE) when compared to those measured in bottlenose dolphins (Kucklick et al. 2002; Struntz et al. 2004). High concentrations of contaminant persistent organic pollutants found in immature dolphins suggest an off-loading of the contaminant from mothers to calves (Kucklick et al. 2002).

Oceanic debris represents an additional threat to *S. bredanensis*. An emaciated individual that was live-stranded in Brazil had ingested 2 plastic bags (Oliveira de Meirelles and Duarte do Rego Barros 2007). Plastic bags also have been found in the stomachs of stranded individuals from Hawaii and Virginia (Walker and Coe 1990).

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